

REPARTITION OF *MAIRIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

The genus *Mairia* Nees, as recently treated or discussed, includes three disparate elements, each essentially restricted to South Africa. The typical element of the genus comprises three species and is here hypothesized to be a member of the subtribe Hinterhuberinae. One of the remaining species is treated within the genus *Gymnostephium* as ***G. papposum*** Nesom, *nom. nov.* (= *Mairia corymbosa* Bolus, not *G. corymbosum* [Turcz.] Harvey). The other ten species, including both blue/white-rayed and yellow-rayed taxa, are treated as *Zyrphelis* Cass. (including *Homochroma* DC.). In addition to the nomenclature already available for *Zyrphelis*, four new combinations are proposed: ***Z. angolensis***, ***Z. decumbens***, ***Z. montana***, and ***Z. perezoides***. *Zyrphelis* is closely related to *Gymnostephium* and *Polyarrhena*, as well as to *Felicia* and other genera primarily centered in South Africa, but it is distantly related to the Hinterhuberinae. Taxonomic summaries are presented for *Mairia*, *Zyrphelis*, and *Gymnostephium*.

KEY WORDS: *Mairia*, *Zyrphelis*, *Gymnostephium*, *Polyarrhena*, Hinterhuberinae, Astereae, Asteraceae

The genus *Mairia* Nees has been recognized by Grau (1971, 1973) as a member of the group of primarily South African genera closely related to *Felicia* Cass. Zhang & Bremer (1993) did not comment on the definition of *Mairia* but accepted Grau's phylogenetic disposition of the genus, positioning it within the group of related genera, including *Felicia*, that they referred to as the "*Amellus* [L.] group." While it is apparent that most of the species currently treated as *Mairia* are part of the *Amellus* group, Harvey (1865, p. 64) noted that the genus comprises "plants associated by an artificial character, the feathery pappus," and followed earlier botanists, including Lessing and DeCandolle, in recognizing infrageneric groups. Grau (1971, 1973, 1977) also

observed that *Mairia* is artificial and composed of subgroups united by the production of plumose pappus bristles on the ray and disc achenes. Grau's opinion (1971) that these subgroups should be separated was unequivocal in a "flow-chart" (p. 278) showing the disposition of a small set of generic level taxa. In that chart he indicated that *Mairia* should be divided into two groups: *Mairia* and *Zyrphelis* Cass. These evidently correspond to "*Mairia* group I" and "*Mairia* group II" of his Figure 3 (1971, p. 277). The present study confirms the polyphyletic nature of *Mairia*.

Nees (1832) originally recognized two species within *Mairia* (*M. crenata* and *M. perezoides*, see taxonomic summary below). DeCandolle (1836) recognized the segregate *Homochroma* DC. but consolidated a number of other species into *Mairia*. *Homochroma* was subsequently incorporated into *Mairia* by Harvey (1865). Kuntze (1891) recognized that Cassini's name *Zyrphelis* predates *Mairia*, and, apparently assuming that all of the species involved represent a single natural group, he made a number of nomenclatural transfers from the latter to the former. The two taxa, however, are heterotypic and their names apply to two of the species groups within *Mairia* that are here hypothesized to be of different phyletic affinity.

Mairia is here reduced to a genus of three species; other species heretofore treated as *Mairia* are distributed between *Zyrphelis* and *Gymnostephium*, which appear to be closely related between themselves but not to *Mairia* sensu stricto. Following is a synoptic account of the three species groups among those taxa generally recognized as *Mairia* (sensu lato), with an indication of their disposition proposed in the present study. A taxonomic summary of the species of each genus is presented at the end of the paper.

1. Herbs with a vestiture of flexuous, thin-based hairs; stems monocephalous, scapose; leaves thick, broadly obovate (10-35 mm wide), in a basal rosette; heads 15-25 mm wide; phyllaries completely herbaceous, flat; ray flowers with broad (3-5 mm), weakly coiling ligules, commonly with staminodia; disc flowers with fertile ovaries; achenes narrowly oblong to oblong-oblancoelate, (2-3-)4-6-nerved, flattened but plump, the surface tan at maturity, glandular and often densely strigose-sericeous, the achenial "twin-hairs" with terminal cells highly uneven in length and strongly divergent; pappus persistent, of 1-2 series of plumose bristles, or with inner series of bristles and an outer series of long scales.
 *Mairia*

1. Subshrubs or basally lignescent herbs with vestiture of stout, thick-based, usually spreading hairs, sometimes also lightly tomentose; stems prominently branching with numerous heads, less commonly monocephalous; leaves linear, almost all cauline or less commonly mostly basally disposed; heads 3-12(-18) mm wide; phyllaries with broad, scarious margins,

strongly concave; ray flowers with narrow (1.0-2.5 mm), tightly coiling ligules, without staminodia; disc flowers with sterile ovaries (fertile in *Zyrphelis perezoides* [Less.] Nesom); achenes oblong-obovate, 2-nerved, strongly flattened, the surface black at maturity and minutely "pebbled", eglandular, sparsely to densely invested with "twin-hairs" with terminal cells even in length and connate to the apex or nearly so, the twin-hairs either (a) filiform or (b) very short and obovate, appearing white-papillate, or the twin-hairs absent; pappus of basally caducous bristles in a single series. (2)

2. Fertile achenes moderately to densely strigose-sericeous with filiform hairs; rays white to blue, or yellow; pappus of ray achenes similar to that of disc (sterile) achenes, of plumose bristles. *Zyrphelis*
2. Fertile achenes moderately to densely invested with short, white papillae, or glabrous to glabrate; rays white to blue; pappus of ray achenes lacking or of only 1-2 plumose or short-serrate bristles (with numerous bristles in one species), disc (sterile) achenes with more bristles. *Gymnostephium*

The position of *Zyrphelis* and *Gymnostephium*

A diagram of relationships among genera of the *Amellus* group by Grau (1973, p. 251) indicates "*Mairia pro parte*" (certainly referring to *Zyrphelis*) most closely resembles the genus *Gymnostephium*, although the diagram implies that *Mairia* p.p. and *Gymnostephium* are each perhaps derived independently from species of *Felicia*. Indeed, *Gymnostephium* is similar to typical *Zyrphelis* in features of habit and vestiture as well as leaf, floral, and achenial morphology. The two genera are notably similar in the consistent ovarian sterility of their disc flowers (except for *Z. perezoides*), their minutely pebbled achene surfaces, and their production of plumose pappus bristles; both are genera mostly restricted to South Africa.

The features common to *Zyrphelis* and *Gymnostephium* that are divergent from *Mairia* are congruent with morphology characteristic of the *Amellus* group. Especially notable among these features are the caducous pappus elements, usually a single series of bristles (of scales and bristles in *Amellus*, *Chrysocoma* L., and *Engleria* O. Hoffm., but the bristles still basally caducous); some species of *Felicia*, however, have persistent bristles. Disc flowers with abortive ovaries occur in all species of *Gymnostephium* Less., all but one of *Zyrphelis*, and some species of *Felicia*, *Polyarrhena* Cass., and *Nolletia* Cass. Achenes in the *Amellus* group are mostly obovate and flat with two, thickened, lateral ribs; they are eglandular, except in *Nolletia*, where achene surfaces are "pocked" and glandular-appearing.

Gymnostephium is distinctive in its reduced pappus, the bristles varying from barbellate to slightly or prominently plumose: the disc achenes (sterile) usually have 2-3 bristles, while the ray achenes are either epappose or produce 1-2 bristles. In *Zyrphelis*, the pappus of both ray and disc achenes is represented by a single series of 8-12 bristles.

One species of *Felicia*, which represents the monotypic genus *Charieis* Cass. (*C. heterophylla* Cass. = *F. heterophylla* [Cass.] Grau), also has plumose pappus bristles, although the plumose lateral extensions are produced mostly on the upper half of the bristles, compared to the entire length of the bristles in *Zyrphelis* and *Gymnostephium*. The ray achenes of *Charieis* are epappose and also are commonly sterile. *Charieis* has been transferred into a subgroup of *Felicia* (Grau 1973) where it appears to fit in chromosome number and other aspects of morphology. Outside of the African species, plumose pappus bristles occur in *Monoptilon* Torr. & Gray of the western United States and, to a reduced degree, in few species of *Vittadinia* A. Rich. of the Australasian region. *Monoptilon* is similar in many respects to the *Amellus* group and apparently closely related to it (Nesom in prep.); *Vittadinia* is not closely related to either the *Amellus* group or to *Mairia* sensu stricto and its putative relatives, as hypothesized here.

The faces of mature achenes of *Gymnostephium* and *Zyrphelis* become minutely pebbled, an easily visible feature with 10-20 \times magnification. Grau (1971) described these distinctive epidermal cells of *Mairia* achenes as "plaster-like." The most reliable distinction between *Zyrphelis* and *Gymnostephium* is in the nature of their achenial vestiture. The achenes of *Zyrphelis* are strigose-sericeous with long, filiform twin-hairs; achenes of *Gymnostephium* (for the most part) are densely white-papillate with short twin-hairs with a rounded-clavate apex. Achenes of *G. gracile* Less., *G. fruticosum* DC., and *G. leve* Bolus commonly are glabrous, but those of *G. leve* sometimes produce very short hairs with minutely divergent apices. Another aspect of achenial variation among *Gymnostephium* species is discussed below in connection with *Polyarrhena*.

The nature of achenial vestiture in *Gymnostephium* is more conservative than features of the pappus (number of bristles on ray and disc, degree of "plumosity"). Based on its achenial vestiture, *Mairia corymbosa* Harvey is transferred in the present paper to *Gymnostephium*, as the achenes of *M. corymbosa* are identical to those of most species of *Gymnostephium* (including the typical ones) in their densely white-papillate faces. Harvey (1865, p. 66) noted that *M. corymbosa* is "Almost identical in aspect and foliage with *Gymnostephium corymbosum* [Harvey], but with a very different involucre and copious feathery pappus." The latter species has hispidulous peduncles and phyllaries (vs. glabrous or glabrate in *M. corymbosa*) and pappus bristles with lateral (plumose) extensions much shorter than *M. corymbosa*. There is variability, however, in pappus "plumosity" among other species of *Gymnos-*

tephium, and there is variation in vegetative vestiture among species of both *Gymnostephium* and *Zyrphelis*. The epithet ("papposa") for the newly transferred species refers to the relatively greater number (within *Gymnostephium*) of pappus bristles on each achene.

The ray flowers of all species of *Gymnostephium* produce white to bluish ligules. Within *Zyrphelis*, the yellow-rayed *Z. ecklonis* (DC.) Kuntze, *Z. lasiocarpa* (DC.) Kuntze, and *Z. angolensis* (Chiov.) Nesom are distinct from the otherwise blue- or white-rayed species. *Zyrphelis ecklonis* was originally described as the monotypic genus *Homochroma* DC., but Harvey (1865) noted that there is essentially nothing except ray color to separate this species from its closest relatives (within *Zyrphelis*), and this synonymy has been followed in recent accounts of South African genera.

Resemblance of *Zyrphelis* and *Gymnostephium* to *Polyarrhena*

Zyrphelis and *Gymnostephium* are similar to the genus *Polyarrhena* (Grau 1970) in habit, vestiture (all have a tendency to produce stipitate-glandularity), leaf morphology, and particularly their tendency to produce disc flowers with sterile ovaries. These three genera appear to constitute a natural group apart from *Felicia*. *Polyarrhena* differs from *Zyrphelis* and *Gymnostephium* in its ligules with a purple, abaxial midstripe (vs. without a midstripe), mature achenes of tan color (vs. black) with smooth, glabrous surfaces (vs. minutely pebbled and strigose-sericeous, papillate, or glabrous) and with a conspicuous, apical collar of light-colored tissue, apparently an outgrowth of the top of the achene wall (vs. without a collar), and serrate pappus bristles (vs. bristles plumose to serrate).

The resemblance between *Polyarrhena* and *Gymnostephium* is emphasized by the observation of what appears to be an incipiently but distinctly formed apical collar on both ray and disc achenes of *G. leve* (e.g., *Esterhuysen 33167* - MO!). The plants of this collection produce glabrous, smooth-faced achenes, and while the apical outgrowth is not as thick as the collar found on achenes of typical *Polyarrhena*, they appear to be homologous. The resemblance is so strong, in fact, that *G. leve* may be better placed within *Polyarrhena*.

A hypothesis of close relationship between *Polyarrhena* and *Zyrphelis* is strengthened by the observation of naturally occurring hybrids between *P. reflexa* (L.) Cass. subsp. *reflexa* and *Z. taxifolia* (L.) Nees on the Cape Peninsula of South Africa. According to label notes on *Esterhuysen 31098* (MO!, distributed from BOL), "A number of plants of this hybrid were present at this locality."

The position of *Mairia* sensu stricto

Grau (1973) was not specific regarding the composition or placement of the portion of *Mairia* not immediately related to *Felicia* and *Gymnostephium* (i.e., the species of *Zyrphelis*). *Mairia* sensu stricto, however, is a remarkably distinct genus that appears to be a member of the Hinterhuberinae (sensu Nesom 1993a, 1993b), showing particular similarities in its tomentose vestiture, broad, coriaceous leaves, multiseriate and persistent pappus, and glandular, multi-ribbed achenes. As such it becomes only the fifth genus of this large subtribe known from the Africa-Madagascar region, joining the African *Pteronia* L. and the Madagascan *Rochonia* DC., *Madagaster* Nesom, and *Apodocephala* J. Baker (the position of *Apodocephala* is discussed in detail in a separate paper, Nesom in prep.). Among these genera, *Mairia* most resembles *Madagaster* and *Rochonia* in leaf and achene morphology and *Madagaster* in ligule color. *Mairia* may be a herbaceous derivative of woody ancestors (i.e., *Madagaster* and *Rochonia* and most other members of the subtribe), as is also the case for several South American genera (e.g., *Laestadia* Kunth, *Oritrophium* [Kunth] Cuatr.). Even if *Mairia* sensu stricto should prove to be more closely related to genera among the *Amellus* group or some other, the argument still remains for the closer relation of *Zyrphelis* and *Gymnostephium*, leaving *Mairia* separate.

The group of species referred to by Grau (1971) as the "herbaceous Diplopappi" or in his "flow chart" of genera (1971, p. 278) as "*Aster harveyanus* O. Kuntze and related species" were treated by Lippert (1971, 1973) within the genus *Aster* L. Grau's observation (1971, p. 279) that "there is still lacking a valid generic name for the herbaceous 'Diplopappi'" implies that he would place these in some other genus, but as detailed in a separate discussion (Nesom in prep.), I have not been able to find justification for separating these from true *Aster*. In their flat achenes with glandular surfaces and persistent, biseriate pappus, these African plants resemble *Mairia* sensu stricto, but their similarity to *Aster* seems more immediate.

Taxonomic summaries

Mairia Nees, *Gen. & Sp. Aster.* 247. 1832. LECTOTYPE (designated here):
Mairia crenata (Thunb.) Nees.

Nees included two species in his original circumscription of the genus. *Mairia crenata* is the best known and longest established of these and is here formally designated as the lectotype, following the implicit suggestion by Pfeiffer (*Nom. Bot.* 2[1]:207. 1874.). The spelling of the genus has sometimes been modified to *Mairea* (e.g., Harvey 1865), as the name commemorates M. Maire, an early collector in South Africa, but the original spelling by Nees is justifiably regarded as correct.

Aster subg. *Pteropappus* Less., *Synops. Gen. Comp.* 166. 1832. *Mairia* sect. *Pteropappus* (Less.) DC., *Prodr.* 5:217. 1836. LECTOTYPE (designated here): *Aster crenatus* (Thunb.) Less. (= *Mairia crenata* [Thunb.] Nees).

Lessing included two species (as *Aster*) in his original description of subg. *Pteropappus*: *Mairia crenata* and *Zyrphelis perezoides*. The decision here to lectotypify it as *Mairia* rather than *Zyrphelis* is somewhat arbitrary.

1. *Mairia coriacea* Bolus, Hook. Ic. Pl., ser. 4, 26:tt. 2541. 1899.
2. *Mairia crenata* (Thunb.) Nees, *Gen. & Sp. Aster.* 248. 1832. BASIONYM: *Arnica crenata* Thunb., *Prodr. Fl. Capens.* 2:154. 1800. *Aster crenatus* (Thunb.) Less., *Synops. Gen. Comp.* 166. 1832. *Gerbera crenata* (Thunb.) Ker-Gawl., *Bot. Reg.* 10:t. 855. 1825. *Zyrphelis crenata* (Thunb.) Kuntze, *Rev. Gen. Pl.* 1:374. 1891.
3. *Mairia hirsuta* DC., *Prodr.* 5:217. 1836. *Zyrphelis hirsuta* (DC.) Kuntze, *Rev. Gen. Pl.* 1:374. 1891.

Zyrphelis Cass., *Ann. Sci. Nat. (Paris)* 17:420. 1829. *Elphegea* subg. *Zyrphelis* (Cass.) Less., *Synops. Gen. Comp.* 183. 1832. *Mairia* sect. *Zyrphelis* (Cass.) DC., *Prodr.* 5:218. 1836. TYPE: *Zyrphelis amoena* Cass. (= *Zyrphelis tazifolia* [L.] Nees).

Homochroma DC., *Prodr.* 5:324. 1836. *Mairia* sect. *Homochroma* (DC.) Harvey in Harvey & Sonder, *Fl. Capens.* 3:64. 1865. TYPE: *Homochroma ecklonis* DC. (= *Zyrphelis ecklonis* [DC.] Kuntze).

1. *Zyrphelis angolensis* (Chiov.) Nesom, *comb. nov.* BASIONYM: *Homochroma angolensis* Chiov., *Boll. Soc. Bot. Ital.* 43. 1924.
2. *Zyrphelis burchellii* (DC.) Kuntze, *Rev. Gen. Pl.* 1:374. 1891. BASIONYM: *Mairia burchellii* DC., *Prodr.* 5:218. 1836.
3. *Zyrphelis decumbens* (Schlechter) Nesom, *comb. nov.* BASIONYM: *Mairia decumbens* Schlechter, *Bot. Jahrb. Syst.* 27:199. 1900.
4. *Zyrphelis ecklonis* (DC.) Kuntze, *Rev. Gen. Pl.* 1:374. 1891. BASIONYM: *Homochroma ecklonis* DC., *Prodr.* 5:324. 1836. *Mairia ecklonis* (DC.) Sonder in Harvey & Sonder, *Fl. Capens.* 3:66. 1865.

5. *Zyrphelis foliosa* (Harvey) Kuntze, *Rev. Gen. Pl.* 1:374. 1891. BASIONYM: *Mairia foliosa* Harvey in Harvey & Sonder, *Fl. Capens.* 3:66. 1865.
6. *Zyrphelis lasiocarpa* (DC.) Kuntze, *Rev. Gen. Pl.* 1:374. 1891. BASIONYM: *Mairia lasiocarpa* DC., *Prodr.* 5:218. 1836. *Felicia lasiocarpa* (DC.) Compton, *Trans. Roy. Soc. S. Africa* 19:312. 1931.
7. *Zyrphelis microcephala* (Less.) Nees, *Gen. & Sp. Aster.* 252. 1832. *Mairia microcephala* (Less.) DC., *Prodr.* 5:218. 1836. BASIONYM: *Elphegea microcephala* Less., *Synops. Gen. Comp.* 184. 1832.

Aster nanus E. Mey. ex DC. [*in syn.*], *Prodr.* 5:218. 1836.

The treatments by Nees and Lessing both appeared in 1832, but it is apparent that Nees had seen Lessing's manuscript and credited him with the original authorship of this name. The same is true for *Zyrphelis perezoides* (below).

8. ***Zyrphelis montana*** (Schlechter) Nesom, *comb. nov.* BASIONYM: *Mairia montana* Schlechter, *Bot. Jahrb. Syst.* 27:199. 1900.
9. ***Zyrphelis perezoides*** (Less.) Nesom, *comb. nov.* *Mairia perezoides* (Less.) Nees, *Gen. & Sp. Aster.* 249. 1832. BASIONYM: *Aster perezoides* Less., *Synops. gen. Comp.* 167. 1832.
10. *Zyrphelis tazifolia* (L.) Nees, *Gen. & Sp. Aster.* 250. 1832. BASIONYM: *Aster tazifolius* L., *Pl. Rar. Afr.* 22. 1761. *Mairia tazifolia* (L.) DC., *Prodr.* 5:218. 1836.

Leyssera ciliata Thunb., *Prodr. Fl. Capens.* 2:160. 1800. *Elphegea ciliata* (Thunb.) Less., *Linnaea* 6:126. 1831.

Zyrphelis amoena Cass., *Ann. Sci. Nat. (Paris)* 17:421. 1829.

Mairia pinifolia Sch.-Bip. ex Walp., *Repert. Bot.* 2:955. 1843.

Mairia lasiocarpa Drege ex Harvey & Sonder [*in syn.*], *Fl. Capens.* 3:65. 1865.

Gymnostephium Less., *Syn. Gen. Comp.* 185. 1832. LECTOTYPE (designated here): *Gymnostephium hirsutum* Less.

DeCandolle included two species in his original circumscription of this genus: *Gymnostephium gracile* and *G. hirsutum* Less. As noted above, *G. gracile* has a distinctive resemblance to the related genus *Polyarrhena*, and to avoid a potential problem (should they prove to be congeneric), *Gymnostephium* is here lectotypified with *G. hirsutum*. The latter species has black achenes with white-papillate surfaces and is similar in other features to the majority of other species included in *Gymnostephium*.

Heteractis DC., *Prodr.* 6:468. 1838. TYPE: *Heteractis falcata* DC. (= *Gymnostephium ciliare* (DC.) Harvey in Harvey & Sonder).

1. *Gymnostephium angustifolium* Harvey in Harvey & Sonder, *Fl. Capens.* 3:67. 1865.
2. *Gymnostephium ciliare* (DC.) Harvey in Harvey & Sonder, *Fl. Capens.* 3:68. 1865. BASIONYM: *Felicia ciliaris* DC., *Prodr.* 5:221. 1836.
Heteractis falcata DC., *Prodr.* 6:469. 1838. *Osteospermum falcatum* E. Mey. ex DC. [*in syn.*], *Prodr.* 6:469. 1838.
3. *Gymnostephium corymbosum* (Turcz.) Harvey in Harvey & Sonder, *Fl. Capens.* 3:67. 1865. BASIONYM: *Agathaea corymbosum* Turcz., *Bull. Soc. Imp. Naturalistes Moscou* 24:60. 1851.
4. *Gymnostephium fruticosum* DC., *Prodr.* 5:300. 1836.
5. *Gymnostephium gracile* Less., *Syn. Gen. Comp.* 186. 1832.
6. *Gymnostephium hirsutum* Less., *Syn. Gen. Comp.* 185. 1832.
7. *Gymnostephium leve* Bolus, *Trans. S. African Philos. Soc.* 16:138. 1907.
8. ***Gymnostephium papposum*** Nesom, *nom. nov.* Based on: *Mairia corymbosa* Harvey in Harvey & Sonder, *Fl. Capens.* 3:66. 1865; not *Gymnostephium corymbosum* (Turcz.) Harvey. *Zyrphelis corymbosa* (Harvey) Kuntze, *Rev. Gen. Pl.* 1:374. 1891.

Taxa excluded from *Mairia*, *Zyrphelis*, and *Gymnostephium* or of uncertain position:

Mairia felicioides Hutch. & Corb., Kew Bull. 10:329. 1920. = *Felicia ovata* (DC.) Compton (Grau 1973).

Mairia pustulata Phillips, Ann. S. African Mus. 9:342. 1917.

This species was described as having obovate leaves in a basal rosette, monocephalous stems, bisexual disc flowers, and a plumose pappus. I have not seen specimens of *Mairia pustulata* but it seems likely that these plants may belong in *Felicia* sect. *Dracontium* Grau (sensu Grau 1973).

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